

Climate change does not alter land-use effects on soil fauna communities

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ABSTRACT

Soil organisms are important drivers of the functioning of terrestrial ecosystems and co-determine how these ecosystems respond to human-induced changes in climate and land use. In the present study, we assessed the interacting effects of these two global change drivers on soil faunal communities. We carried out an experimental field study within the framework of the Global Change Experimental Facility (GCEF) manipulating (1) two climatic conditions (ambient vs. future) and (2) five land-use regimes (with two croplands: conventional farming and organic farming; and three grasslands: intensively-used meadow, extensively-used meadow and extensively-used pasture). The future climate treatment is characterized by a slight increase of soil temperature ($\sim 0.5^{\circ}\text{C}$), whereas precipitation was strongly decreased during the summer (by $\sim 20\%$) but moderately increased during spring and autumn (by $\sim 10\%$). Soil fauna was sampled in two consecutive years in spring and autumn. Overall, future climate tended to have negative effects on soil fauna communities. For specific taxa, the detrimental effects of climate change were only evident for Isotomidae (Collembola) and Chilopoda. In general, soil faunal composition differed strongly between grasslands and croplands, with a higher number of macrofauna taxa and generally higher abundances of meso- and macrofauna in grasslands. However, land-use intensity within these land-use types had no further effect. Likewise, there were negligible interactive effects of climate and land use, and short-term effects of projected climate change on the community compositions of soil fauna were found to be more subtle than land-use effects. Land-use effects on soil fauna are therefore equally strong under ambient and future climatic conditions.

1. Introduction

Soil biota fulfill different functional roles and drive many essential ecosystem processes (Menta, 2012). The soil mesofauna comprises important secondary decomposer organisms (e.g., Collembola and Oribatida) that provide the basis for soil fertility and nutrient availability by mineralizing organic matters and thereby supporting the growth of microbes and plants (Wang et al., 2017; Wickings and Grandy, 2011). Simultaneously, soil fauna can modify the community composition of microbes and thus affect early stages of litter decomposition and other microbial processes (Coleman and Wall, 2015; García-Palacios et al., 2013). Similarly, soil macrofauna profoundly enhances litter fragmentation and soil aggregation, and indirectly promotes water and nutrient infiltration as well as gaseous emissions (Ayuke et al., 2011; Lavelle

et al., 2001). Given these critical ecosystem functions, soil fauna are gradually becoming a key research frontier in the context of global change (Coyle et al., 2017).

Some soil fauna groups (e.g., Collembolans) are often used as bioindicators to evaluate soil quality since they are quite sensitive to environmental changes, which is reflected by shifts in their abundance and community composition (Lavelle et al., 2006; Lindberg et al., 2002). Worldwide, climate change has become a main topic for soil ecological research (Eisenhauer et al., 2017), and the functions provided by soil fauna have been found to be climate-dependent (García-Palacios et al., 2013; Wall et al., 2008). Future climate models predict a general increase in temperature with rising greenhouse gas emissions, lower precipitation, especially in summer, and more extreme weather events, like droughts, in many parts of the world (IPCC, 2014). Climate

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change has highly variable effects on soil faunal communities with differences in the direction as well as magnitude of effects depending on local conditions and taxonomic groups (Blankinship et al., 2011; Coyle et al., 2017; Wu et al., 2014). Furthermore, a recent study demonstrated that different climate change drivers interactively influence the functioning of soil faunal communities, as warming had negative effects on the feeding activity of soil detritivores only in combination with reduced precipitation (Thakur et al., 2018), which is a common scenario in many climate change models. Hence, future climatic conditions may impair key soil processes (e.g., decomposition) by decreasing the activity of detritivores (Yin et al., 2019).

Climate and land-use changes have been ranked as the biggest threats to global biodiversity (Sala et al., 2000). Moreover, land-use change potentially leads to feedback effects (de Chazal and Rounsevell, 2009). Soil faunal feeding activity and soil food webs have been shown to be particularly vulnerable to land-use change (Tao et al., 2016; Tsiafouli et al., 2015). Current land-use change is mainly driven by two ongoing processes: first, a conversion of land-use types, usually from complex natural or semi-natural systems to simplified agricultural systems; and second, land-use intensification within certain land-use types (McLaughlin and Mineau, 1995). Both factors may significantly influence the diversity, abundance, and community composition of soil fauna (Baker, 1998; Postma-Blaauw et al., 2010) with potential consequences for ecosystem functions like primary production (Cardinale et al., 2004). There are increasing concerns regarding the sustainability of simplified farming systems (Bardgett and Van Der Putten, 2014; Wall et al., 2015) and how they will respond to climate change. Generally, soil food webs in grasslands are more resistant and adaptable to drought compared to croplands (De Vries et al., 2012). This indicates that responses of soil biota to climate change can be modulated by different land-use types. Given the potentially strong influence of climate and land use, it is surprising that so far little effort has been made to investigate the potential interaction between climate and land use on soil fauna communities (de Chazal and Rounsevell, 2009). Here, we address this gap by studying soil meso- and macrofauna in a large-scale field experiment crossing two climate scenarios (ambient vs. future) with five different land-use regimes (with the two land-use types croplands and grasslands differing in management intensity). Our aim is to answer the following question: What are the effects of climate change on the diversity, abundance, and community composition of soil fauna and how are they altered by land-use type (croplands vs. grasslands) and management intensity?

2. Materials and methods

2.1. Field site

The study was conducted in 2015 and 2016 at the Global Change Experimental Facility (GCEF), which is located at the field research station of the Helmholtz-Centre for Environmental Research in Bad Lauchstädt, Saxony-Anhalt, Germany ($51^{\circ} 23' 30''$ N, $11^{\circ} 52' 49''$ E, 116 m a.s.l.). This experimental platform was established on a former arable field with the last crop (oat) on all subplots in 2013, and it is characterized by a low mean annual rainfall (498 mm) and a mean temperature of 8.9°C . The soil of the study site is Chernozem. This highly fertile soil type is typically developed upon carbonatic loess substrate under summer-dry climatic conditions and characterized by a high content of humus (in Bad Lauchstädt 2%) down to a depth of > 40 cm, a high water storage capacity (31.2%) and storage density (1.35 g/cm³). Furthermore, high nutrient contents (like N, P and K) together with a soil pH of ~ 7.0 lead to favorable soil conditions for flora and fauna (Altermann et al., 2005).

2.2. Experimental set-up

The GCEF has been established on a former arable field which was

homogenously cultivated for decades and comprises 10 mainplots (80 m \times 24 m) with each mainplot consisting of 5 subplots (each 16 m \times 24 m). The minimum distance between the mainplots is 25 m. The five subplots per mainplot (in total 50) are randomly assigned to one of the five land-use regimes: (1) conventional farming, (2) organic farming, (3) intensively used meadows, (4) extensively used meadows and (5) extensively used pastures with sheep grazing (for detailed description see Table S1). All land-use regimes were established by seeding in 2013. Half of the mainplots are subjected to an ambient climate scenario, the other half to a future climate scenario. This results in a split-split-plot design with climate as mainplot factor and land use as subplot factor (five replicates per climate \times land use combination).

All subplots are equipped with steel framework elements with a total height of 5.50 m allowing the use of agricultural machines. Within the mainplots subjected to future climate, all subplots are equipped with plastic tarpaulins serving as roofs and side panels on the longer sides of the subplots which are automatically closed from sundown to sunrise to increase night temperatures. Further, rain sensors allow for the modulation of water supply by opening or closing the roofs and an irrigation system, fed by a large water reservoir, was installed as potential additional water source. To avoid possible side effects of the construction itself, steel frameworks were also established on all subplots within mainplots with ambient climate treatment. Subplots within the mainplots are separated from each other by translucent plastic blinds ranging from 50 cm belowground to 50 cm aboveground.

The future climate treatment is based on climatic conditions predicted for Central Germany in the period from 2070 to 2100. It resembles a consensus scenario derived from 12 climate simulations based on four different emission scenarios using three established regional climate models: COSMO-CLM (Rockel et al., 2008), REMO (Jacob and Podzun, 1997) and RCAO (Dösscher et al., 2002). Whilst the mean temperature was projected to increase over all seasons of the year by 1 to 2°C , the amount of precipitation was predicted to strongly decrease in summer and slightly increase during the rest of the year. For this, mean values of the 12 projections were calculated resulting in a precipitation change of about +9% in spring (March–May) as well as in autumn (September–November) and about -18% in summer (June–August). For this, every week and after stronger rain events, we added the amount of water to reach $\sim 110\%$ of total rain under ambient conditions to the subplots with future climate in spring and autumn. In summer, the rain sensor together with the irrigation system was used to adjust precipitation on the subplots with future climate to $\sim 80\%$ of ambient rainfall. In 2015, precipitation was increased by 9.3% and 9.2% in spring and autumn, respectively, and reduced by 21% in summer on the subplots with future climate. In 2016, precipitation was increased by 13.6% and 9.2% in spring and autumn, respectively, and decreased by 19.7% in summer (Fig. S1A). To apply the temperature treatment on future climate mainplots, roofs and side panels were closed during 80% of the total night time from February 15th to December 11th in 2015 and from March 22nd to November 29th in 2016.

Roofs and side panels are also used to apply a passive nighttime warming to the subplots (Beier et al., 2004), in case of strong frosts and high wind speed. The roof phases were from February 15th to December 11th in 2015 and from March 22nd to November 29th in 2016. This night closing resulted in an increase of the daily mean of air temperature close to the ground (5 cm height) by 0.55°C across the roof phases, in a depth of 1 cm by 0.62°C , and in a depth of 15 cm by about 0.50°C . Near-surface soil temperatures in a depth of 1 cm showed a certain dependency on land-use regime with a trend toward higher temperatures in the grasslands (Fig. S2A). The mean increase of daily soil temperature due to roof closing in the night varied among the land-use regimes between 0.20°C and 0.43°C (Fig. S2B). Mean soil water content mainly followed the ambient rain pattern and was affected by the precipitation treatment, but showed no obvious differences between land-use regimes (Fig. S1B–F).

Croplands and intensively used meadows were established on the

Table 1

Mesofauna responses to climate, land use, date and their interactions. Results (*F*-values) of the split-plot generalized linear mixed model (type III sum of squares) with repeated measures on number of taxa, total abundance, Pielou's evenness of mesofauna, as well as the abundances of Collembola groups and Acari groups.

Independent variable	Df	Number of taxa	Total abundance	Pielou's evenness	Coll	Isot	Ento	Kati	Smin	Onyc	Hypo	Acar	Orib	Meso	Pros
Climate (C)	1,8	2.57	2.37	0.09	5.2 ⁺	10.67*	4.64 ⁺	0.06	0.07	0.99	0.02	0	0.03	0	1.91
Land use (L)	4,32	0.78	11.6***	0.29	2.69*	1.2	4.48**	1.75	4.75**	1.49	0.64	8.95***	6.28***	5.74**	3.89*
Date (D)	3,24	4.86**	8.04***	0	27.89***	42.68***	15.65***	6.94**	10.33**	5.36*	2.89	10.22***	12.07***	7.2*	96.98***
C × L	4,32	0.43	0.63	0.02	1.4	0.29	0.55	1.08	0.37	0.17	0.41	0.35	0.52	0.28	0.35
C × D	3,24	0.07	0.74	0.05	0.18	0.32	3.39*	1	0.71	0.21	0.31	1.9	1.74	0.31	2.95
L × D	12,96	1.14	3.12***	0.02	5.51***	4.13***	1.56	2.65**	3.5***	1.51	2.01*	1.64	1.89*	0.98	3.23***
C × L × D	12,96	0.13	0.64	0.01	0.32	0.54	1.14	1.19	0.55	0.98	0.54	1.32	1.19	0.7	0.74

Abbreviations: Coll: Collembola; Isot: Isotomidae; Ento: Entomobryidae; Kati: Katiannidae; Smin: Sminthurididae; Hypo: Hypogastruridae; Onyc: Onychiuridae; Acar: Acari; Orib: Oribatida; Pros: Prostigmata; Meso: Mesostigmata.

* *F*-values with $P < 0.05$.

** *F*-values with $P < 0.01$.

*** *F*-values with $P < 0.001$.

+ *F*-values with $P < 0.1$.

respective subplots in summer/autumn of 2013. Plants for the extensively used meadows and pastures were repeatedly sown during spring and autumn of 2014. The temperature treatment started in April 2014 in all land-use regimes; however, to homogenize moisture conditions during the establishment of seedlings of grassland plants, roofs stayed open during rain. The manipulation of precipitation started in July 2014 for all land-use regimes. A more detailed description of the facility and the concept of the project can be found in Schädler et al. (2019).

2.3. Collection and identification of soil fauna

Soil fauna samples were taken twice per year in spring and autumn of 2015 and 2016. Thus, the first sampling was done one year after the initiation of the climate treatment. On each sampling date, three soil core samples (\varnothing 6 cm, 5 cm depth) were taken per subplot to extract mesofauna (mostly Collembola and Acari) using a Macfadyen high-gradient extractor (Macfadyen, 1961). Collembolans were determined to family level and Acari to order level using a VHX-Digital microscope. Macrofauna was sampled with two soil cores (\varnothing 16 cm, 5 cm depth) per subplot and extracted through a 10 days gradual increase in temperature using a Kempson extraction method (Kempson et al., 1963). Soil macrofauna was determined to family level (Staphylinidae, Carabidae and Formicidae), order level (Diptera, Araneae, Isopoda, Haplotauxida, Julida and Psocoptera) or class level (Chilopoda, Araneae, Symphyla and Gastropoda), respectively.

2.4. Statistical analysis

The datasets of soil meso- and macrofauna were based on the mean values per sampling date and per subplot. Number of taxa (diversity), total abundance, Pielou's evenness, and the abundances of specific taxa were calculated and then analyzed using a repeated-measures split-plot general linear mixed models with type III sum of squares in SAS (University Edition v9.4). Count data was analyzed assuming Poisson-distributed residuals with log-link function. There was no indication for overdispersion of data, and assuming alternative distributions (including negative binomial) resulted in inferior model fit (assessed via Akaike Information Criterion). The same analyses were applied to data on the abundances of single taxa which could be found in at least half of the samples. Post hoc Tukey's HSD tests were carried out to reveal significant differences among the respective levels within factors.

To assess a possible general trend of climate treatment across all taxa of soil fauna, we calculated Cohen's *d* as effect size of climate effect for all taxa (Lakens, 2013) and the 95% confidence intervals to test for significant deviation from zero. The effect of land use was not examined using this approach since there is no possibility to define differences

across 5 different levels as negative or positive effects.

To analyze the relationships between meso- and macrofaunal community composition and the two experimental factors (climate, 2 levels and land use, 5 levels; both categorical), redundancy analyses - RDA (Rao, 1964; van den Wollenberg, 1977) using standardized abundance data were carried out using R 2.1.4.2., package vegan (Oksanen et al., 2015). We checked for linear relationships in the data sets (Euclidean metric; prerequisite for this method) by conducting detrended correspondence analyses (DCA) and identifying the respective longest gradient. As these were always below 3, the use of linear methods is appropriate (Lepš and Šmilauer, 2003). Significance of ordination axes and environmental variables were tested using Monte Carlo permutation tests (999 permutations). Only land-use types showed significant correlations with the community composition of meso- and macrofauna; so, we used one-way permutational multivariate analysis of variance - PERMANOVA (Anderson, 2001) based on abundance data and Bray–Curtis distances to test for significant differences in meso- and macrofaunal community compositions between different land-use regimes (overall and pairwise comparisons). Statistical significances were based on 999 permutations. Bonferroni-corrected *P* values were used because more than two groups were compared. Each pair of land-use regimes showing significant differences in their meso- and/or macrofaunal community composition in the PERMANOVA was further analyzed using Similarity Percentages - SIMPER (Clarke, 1993). This enabled us to identify the respective soil fauna taxa, which mainly generated the dissimilarity patterns between two land-use types (croplands and grasslands). PERMANOVA and SIMPER analyses were conducted with the program "PAST" (Hammer et al., 2001).

3. Results

3.1. Climate and land-use effects on ecological indices of meso- and macrofauna

There was a general trend toward more macrofauna taxa and higher abundances in the grasslands compared to the croplands, and the number of taxa and total abundance of meso- and macrofauna tended to be lower under future climate, though the difference from ambient climate was not significant (Tables 1, 2; Fig. 1A, B). Land-use treatments significantly affected the number of macrofauna taxa (Table 2) as well as the total abundances of meso- and macrofauna (Tables 1, 2), but the specific pattern and the magnitude differed between sampling dates (land use × date interaction, Tables 1, 2). In general, the number of macrofauna taxa and total abundances of meso- and macrofauna were higher in grasslands than in croplands, and this pattern was especially pronounced in autumn (especially in autumn 2016), when the abundances of both, meso- and macrofauna as well as the number of

Table 2
Macrofauna responses to climate, land use, date and their interactions. Results (*F*-values) of the split-plot generalized linear mixed model (type III sum of squares) with repeated measures to analyze the effects on number of taxa, total abundance, Pielou's evenness of macrofauna, as well as the abundances of selected macrofauna taxa.

Independent variable	Df	Number of taxa	Total abundance	Pielou's evenness	Stap	Stap_A	Stap_L	Cara	Cara_A	Cara_L	Dipt	Dipt_A	Dipt_P	Dipt_L	Chil	Aran	Dipl	DipL	Isop	Form	Symp	Gast	Hapl	Juli	Psoc
Climate (C)	1,8	0.06	0.32	0.11	0.7	0.5	0.38	2.47	1.05	1.72	0.66	0.04	0.11	0.91	5.59*	0.12	0.1	0.42	0.01	2.97	2.4	2.08	0.51	0.05	
Land use (L)	4,32	17.89***	34.45***	0.26	12.34***	8.35***	7.21***	12.58***	4***	2.37	0.62	3.79*	2.09	3.59	6.16***	3.42*	4.95**	1.43	0.6	0.52	1.6	1.31			
Date (D)	3,24	5.88***	8.9***	0.32	5.56*	3.91*	17.2***	3.6*	10.2***	14.39***	6.11***	13.17***	13.28***	2.47	9.8*	8.11***	6.45***	6.24***	3.29*	8.17***	5.37*	2.88	1.58	2.42	
C × L	4,32	0.9	0.89	0.01	1.32	0.87	2.22	0.54	0.66	0.21	0.59	0.56	1.36	0.85	0.91	0.99	0.43	0.82	0.12	2.27	0.51	1.98	1.05	0.95	
C × D	3,24	2.06	1.28	0.02	0.43	0.46	0.37	0.63	0.43	1.72	0.74	0.96	0.96	1.75	3.3*	0.27	0.12	1.21	0.89	2.55	1.84	0.89	1.18	1.11	
L × D	12,96	31.12***	4.83***	0.03	3.7***	3.31***	6.59***	1.41	1.92*	2*	1.72	0.84	1.65	1.62	2.58*	1.74	1.79	2.71*	1.54	1.7	0.43	2.57*	0.94	0.88	
C × L × D	12,96	1.35	1.25	0.02	0.98	0.71	1.62	1.12	1.13	0.71	1.23	0.51	0.66	1.51	0.7	0.63	1.11	1.85	0.96	1.67	0.74	1.6	0.88	1.08	

Abbreviation: Stap: Staphylinidae; Stap_A: Staphylinidae adult; Stap_L: Staphylinidae larvae; Cara: Carabidae; Cara_A: Carabidae adult; Cara_L: Carabidae larvae; Dipt: Diptera; Dipt_A: Diptera adult; Dipt_P: Diptera pupae; Dipt_L: Diptera larvae; Chil: Chilopoda; Aran: Araneae; Dipl: Diplura; Isop: Isopoda; Form: Formicidae; Symp: Symphyla; Gast: Gastropoda; Hapl: Haplotaixida; Juli: Julida; Psoc: Psocoptera.

* *F*-values with $P < 0.05$.

** *F*-values with $P < 0.01$.

*** *F*-values with $P < 0.001$.

macrofauna taxa were significantly higher in the three grassland sites compared to the croplands (Fig. 1C–E). Further, there were no significant climate and land-use effects on Pielou's evenness of meso- and macrofauna (Tables 1, 2). Also, we did not find any significant interactive effects of climate and land use on these ecological indices (number of taxa, total abundance and Pielou's evenness) of meso- and macrofauna (Tables 1, 2).

3.2. Climate and land-use effects on specific groups of meso- and macrofauna

The most abundant mesofaunal groups were Collembola and Acari, with Collembolans accounting for one quarter of the total abundance of mesofauna. Therein, Isotomidae was the dominant family, which made up ~70% of the total Collembola abundance. Under future climate, the abundances of Collembola as well as the Collembolan family Entomobryidae were marginally significantly lower compared to ambient climate (Table 1). The same pattern was found for Isotomidae (Table 1; Fig. 2A). However, the other Collembolan families, including Katiannidae, Sminthurididae, Onychiuridae, and Hypogastruridae, were not significantly affected by the climate treatment (Table 1).

There were significant interacting effects of climate and date on Entomobryidae, which was mostly caused by the high abundance in autumn 2016, where their abundance was significantly higher under ambient compared to future climate (Table 1, Fig. 2B). This might indicate an increasing influence of climate treatment with time; however, we could not find this pattern in other groups of Collembola. There was a general significant effect of land-use type on the total abundance of Collembola and the abundances of specific Collembolan families with higher individual numbers in grasslands compared to croplands (Fig. 2C–D). This effect was especially strong for total Collembola in the first and last sampling (Fig. 2F), whereas for Isotomidae in the first sampling (Fig. 2G) and for Katiannidae in last sampling (Fig. 2H; significant land use × date interaction, Table 1).

Acari made up nearly three quarters of the total abundance of mesofauna, of which Oribatida was the most dominant group accounting for > 70% of total Acari abundance. However, we could not find any significant climate effect neither on the total abundance nor on specific groups of Acari (Oribatida, Mesostigmata and Prostigmata; Table 1). In contrast, we found significantly higher abundances of total Acari and the groups Oribatida, Mesostigmata and Prostigmata in grasslands compared to croplands (Table 1; Fig. 3A–D). For Oribatida, these land-use effects were especially strong in the last sampling (Fig. 3E; significant land use × date interaction, Table 1).

Nearly all taxa of macrofauna did not respond significantly to climate change, except for Chilopoda (Table 2), where future climate significantly decreased their abundance (Fig. S3A), and this effect was most pronounced in autumn 2016 (Table S3B). The responses of single macrofauna taxa to land use were found to differ in magnitude and direction. More specifically, land-use treatments significantly affected the abundances of total Staphylinidae (adults and larvae), total Carabidae (adults and larvae), Diptera pupae, Chilopoda, Hemiptera, Araneae, Diplura, Isopoda and Formicidae (Table 2). All these macrofauna taxa showed generally higher abundances in grasslands compared to croplands (Fig. S4A–L). Total Staphylinidae (adults and larvae), Chilopoda, Diplura, Isotoda and Formicidae tended to be more abundant in extensively used meadows than in intensively used meadows and extensively used pastures, whilst the abundance of Carabidae (adults and larvae), Diptera pupae and Araneae decreased from extensively-used pastures over extensively-used meadows to intensively-used meadows. Additionally, the land-use effects on abundances of Staphylinidae (adults and larvae), Carabidae (adults and larvae), Chilopoda, Isopoda and Haplotaixida, differed according to the sampling dates, with stronger effects in autumn than in spring (Fig. S4M–N; e.g., Staphylinidae and Carabidae adults). Even if there was no significant response of the majority of fauna groups to the climate treatment

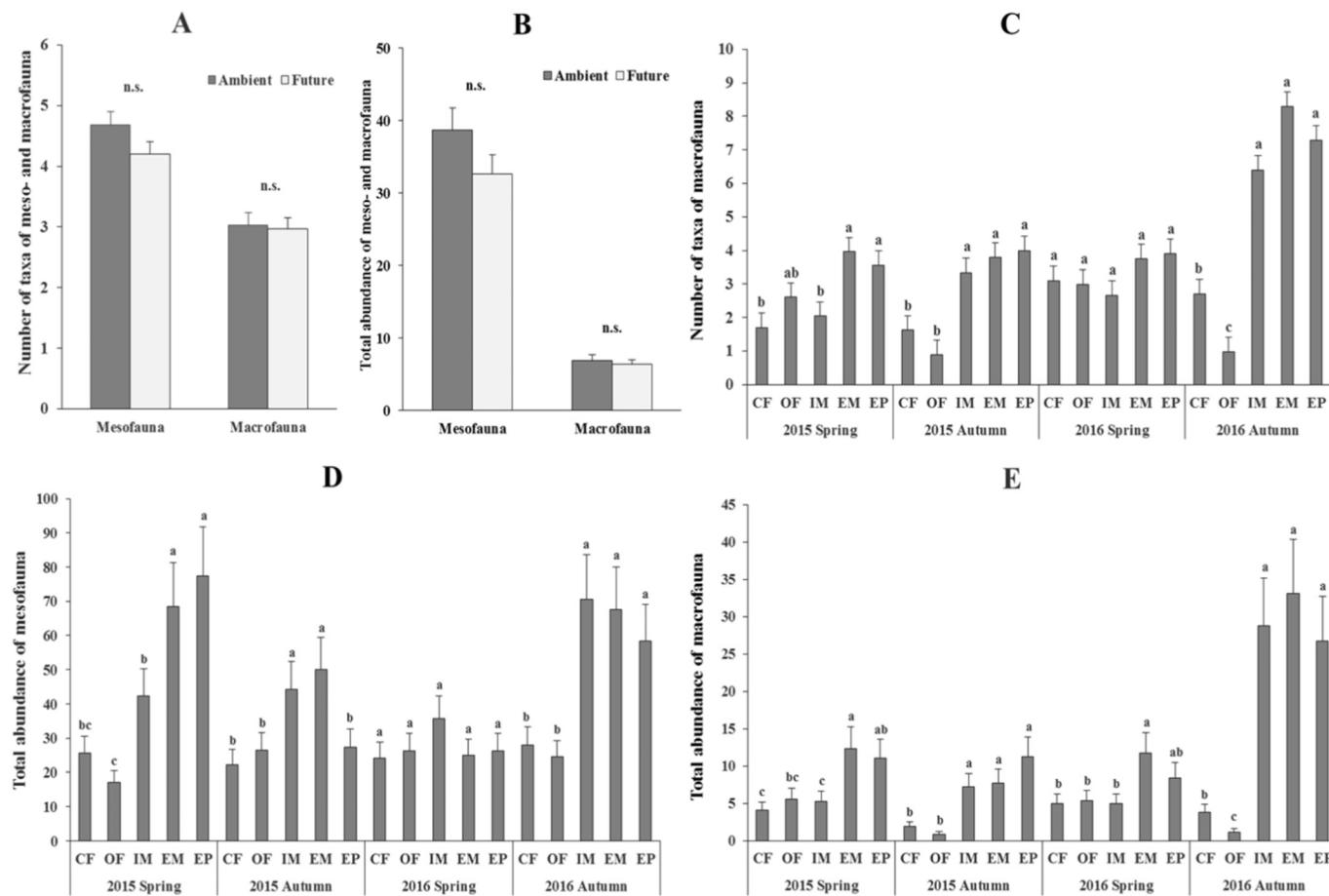


Fig. 1. A: Effects of climate on number of taxa of meso- and macrofauna. B: Effects of climate on total abundance of meso- and macrofauna. C: Effects of land use \times date interaction on the number of macrofauna taxa. D: Effects of land use \times date interaction on the total abundance of mesofauna. E: Effects of land use \times date interaction on the total abundance of macrofauna.

Notes: Values as Mean \pm SE, and all significant differences were revealed by one-way ANOVA with Tukey's Post-hoc-test (the same as below). A-B: n.s. represents non-significant differences between ambient and future climate treatments. G-E: Different lowercase letters represent significant differences among land-use regimes in the same date. Land-use regimes are abbreviated (the same as below) as CF for conventional farming, OF for organic farming, IM for intensively used meadows, EM for extensively used meadows and EP for extensively used pastures.

according to the GLMM, there was a general negative response across all taxa to climate change (Table S2, mean Cohen's $d = -0.45$, 95% confidence interval: lower limit = -0.80 , upper limit = -0.10).

3.3. Climate and land-use effects on community composition of meso- and macrofauna

Land-use treatments significantly affected the community composition of soil meso- and macrofauna, whilst there was no significant climate effect (Fig. 4A, B). The climate effect was therefore excluded from the analyses. For mesofauna, 20.76% of the total variance in the data set was explained by the five constrained RDA axes (Table S2). RDA 1 significantly explained 62.47% of this variance (Fig. 4A; Tables S3, S4) and represented mostly the intensively used meadows (Table S5—highest absolute value at RDA 1). Katiannidae got the highest species score (Table S6). The RDA 2 accounted for 30.14% of explained variance (Fig. 4A; Tables S3, S4), and represented mostly the extensively used meadows (Table S5—highest absolute value at RDA 2), and Sminthurididae got the highest species score (Table S6).

For macrofauna, 21.35% of the total variance in the data set was explained by the five constrained RDA axes. The RDA 1 significantly explained 66.47% of this variance (Fig. 4B; Tables S3, S4) and represented mostly the organic farming (Table S4—highest absolute value at RDA 1), and adult Carabidae got the highest species score (Table S6). The RDA 2 accounted for 14.41% of the explained variance

(Fig. 4B; Tables S3, S4), and represented mostly the intensively used meadows (Table S6—highest absolute value at RDA 2), and Diptera larvae got the highest species score (Table S6).

The results from PERMANOVA showed that the significant land-use effect on the community compositions of meso- and macrofauna were driven by land-use type (croplands vs. grasslands) and not by land-use management intensity within the same land-use type (Table S7). SIMPER analysis confirmed that the community compositions of meso- and macrofauna were moderately to strongly different between croplands and grasslands. The overall dissimilarity ranging from 47.83% (mesofauna, conventional farming vs. extensively used pastures) to 94.75% (macrofauna, organic farming vs. extensively used meadows). Detailed information on percent dissimilarity and top 5 taxa of soil meso- and macrofauna that contributed the most to the observed difference in the communities between croplands and grasslands are shown in Table S8.

4. Discussion

4.1. Climate effects on soil fauna

Climate change may alter the activity of soil biota (fauna and microbes) by changing soil microclimate, and thereby ecosystem functions, such as litter decomposition (Allison et al., 2013; Yin et al., 2019). In separate analyses, the number of taxa, evenness and the

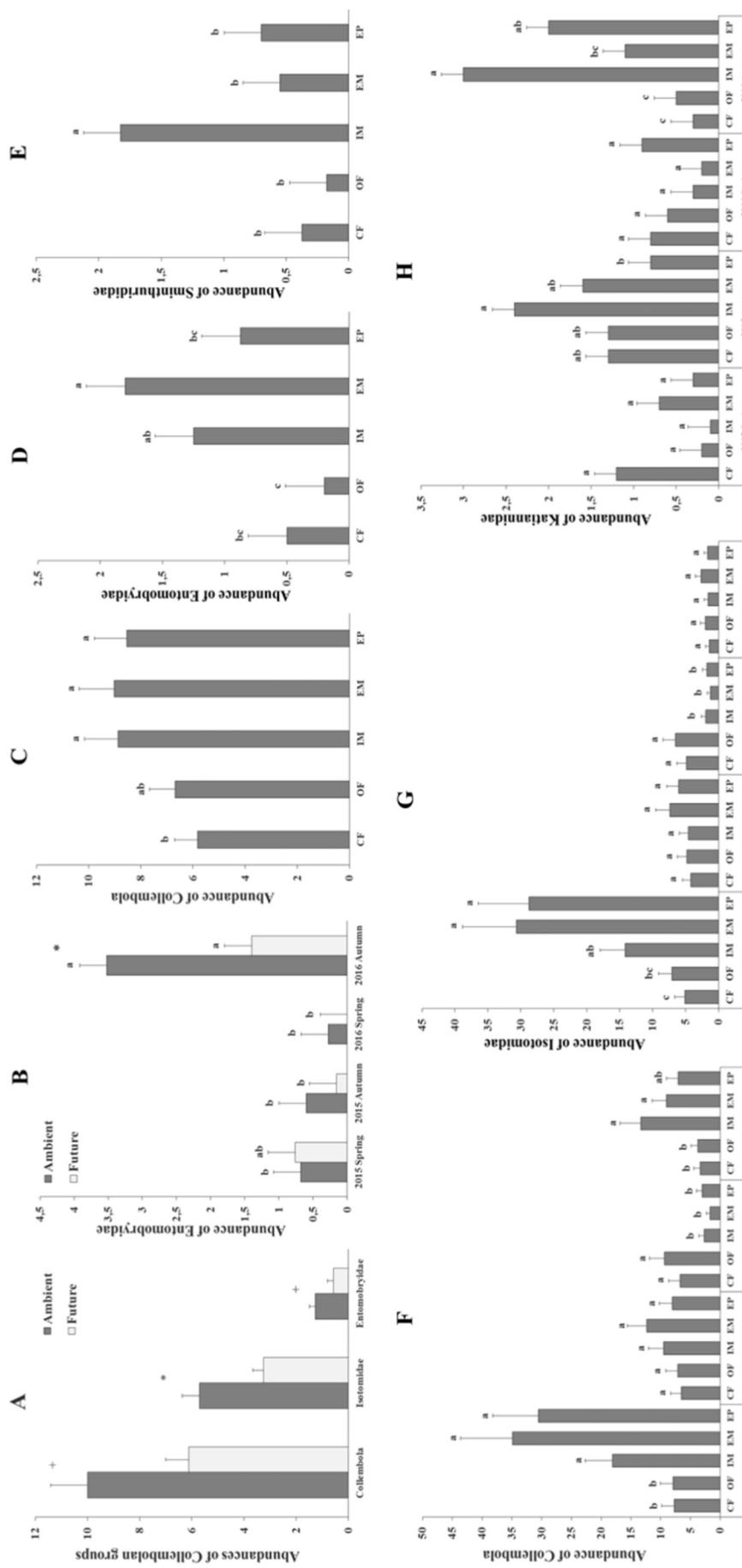


Fig. 2. A: Effects of climate on the abundances of Collembolan groups (Collembola, Isotomidae and Entomobryidae). B: Effects of land use on Sminthuridae abundance. C: Effects of land use × date interaction on the abundance of Entomobryidae. D: Effects of land use on Sminthuridae abundance. E: Effects of land use × date interaction on Collenubidae abundance. F: Effects of land use × date interaction on Isotomidae abundance. G: Effects of land use × date interaction on Katiannidae abundance. H: Effects of land use × date interaction on Sminthuridae abundance. Notes: A-B: Significance levels between ambient and future treatments are given as + for $P < 0.1$ and * for $P < 0.05$. Different lowercase letters represent significant differences among different land-use regimes. C-H: Different lowercase letters represent significant differences among different land-use regimes in the same date. For abbreviations of land-use regimes see Fig. 1.

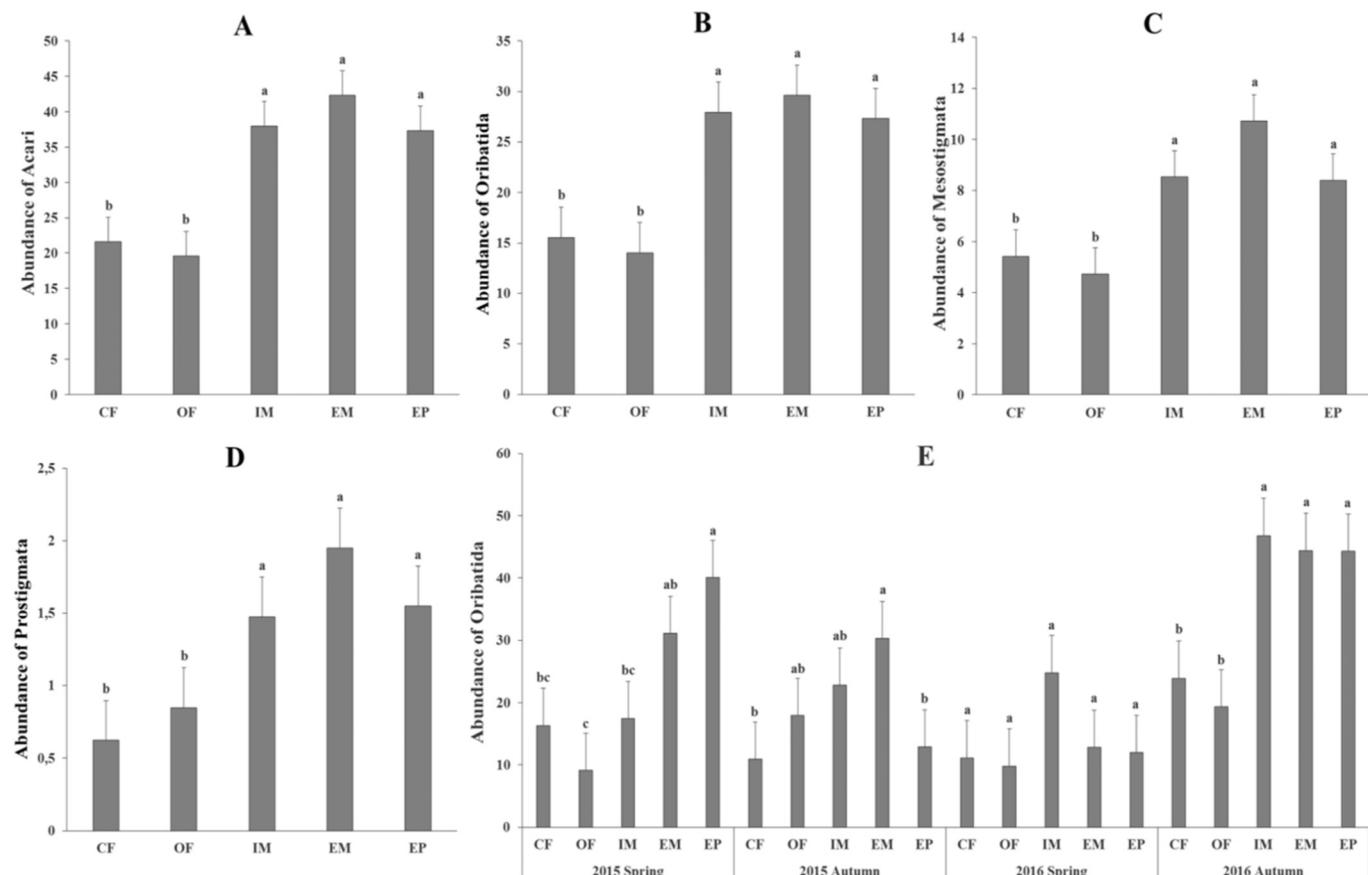


Fig. 3. A: Effects of land use on Acari abundance. B: Effects of land use on Oribatida abundance. C: Effects of land use on Mesostigmata abundance. D: Effects of land use on Prostigmata abundance (mean + SE). E: Effects of land use × date interaction on Oribatida abundance.

Notes: A–D: Different lowercase letters represent significant differences among different land-use regimes. E: Different lowercase letters represent significant differences among land-use regimes in the same date. For abbreviations of land-use regimes see Fig. 1.

abundance of fauna in total as well as most taxa showed no significant responses, whilst we found a decrease in Collembolan abundance under future climatic conditions. This result is in accordance with Makkonen et al. (2011) who found Collembola to be vulnerable to soil desiccation under future climate. As warming exacerbates the effects of drought (Thakur et al., 2018; Vestergård et al., 2015), these drought periods, in particular, are likely to be the main driving force behind the decline of Collembola rather than the temperature increase itself (Hodkinson et al., 1998). Larger-sized epedaphic Collembola are generally more drought-tolerant and may better survive under future climatic conditions than the more hydrophilic, smaller-sized euedaphic species (Makkonen et al., 2011). In contrast, we found that the future climate treatment only tended to decrease the abundances of larger-sized Collembola (i.e., Isotomidae and Entomobryidae), whereas the smaller-sized Collembola (i.e., Katiannidae, Sminthurididae, Onychiuridae and Hypogastruridae) were less affected. Hence, epedaphic Collembola with larger body size were more susceptible to our climate treatment than epedaphic Collembola with smaller body size or euedaphic families. Our results are basically in line with those of Jucevica and Melecs (2006), who demonstrated that climate change-induced drought negatively and profoundly affected litter-dwelling Collembola, especially epedaphic species, because the soil surface is more vulnerable to environmental fluctuations compared to deeper soil layers.

Besides Collembola, Acari are frequently used as bioindicators for environmental assessments (Behan-Pelletier, 2003). Similar to Collembolans, drought can decrease the species richness and abundance of Acari. Especially vulnerable are species of the order Oribatida (Lindberg et al., 2002), which was one of the most dominant groups in our study, accounting for around three quarters of total Acari

abundance (followed by Mesostigmata and Prostigmata). However, our results showed that future climatic conditions had no significant effects neither on Oribatida nor on Mesostigmata or Prostigmata. In line with our findings, Acari were reported to be less drought-sensitive than Collembola (Vestergård et al., 2015), whilst soil mesofauna may be generally unaffected even by long-term manipulations of climate (Holmstrup et al., 2013). However, Holmstrup et al. (2013) also suggest that annual drought events can alter the community structure of Collembola without detectable effects on the Acari community. Thus, our study adds to the body of evidence that Acari might be less sensitive to changes in climatic conditions.

Further, most macrofauna taxa showed no response to climate change in the present study, except for Chilopoda, whose abundance decreased under future climatic conditions. Whilst this might be a direct effect of drought, it is also plausible that this predatory group suffers from the climate change-induced decline in Collembola density, i.e., from bottom-up induced changes in the soil food web (Crowther and Grossart, 2015). A non-random loss of top predators in soil communities has been found under drought conditions and warming (Lindo et al., 2012), leading to corresponding trophic cascade prey release (Staddon et al., 2010). Future studies should address how biotic interactions and the balance of bottom-up versus top-down forces shifts in soil food webs in a changing world. We are aware that several groups of macrofauna (e.g., Diptera, Coleoptera) may have a higher mobility and can move among the experimental plots. Any effects of experimental treatments can therefore be considered as conservative measures of the real effects. However, we could not observe generally weaker effects of climate change on macrofauna compared to mesofauna in this study.

Soil fauna is known to be strongly dependent on soil moisture

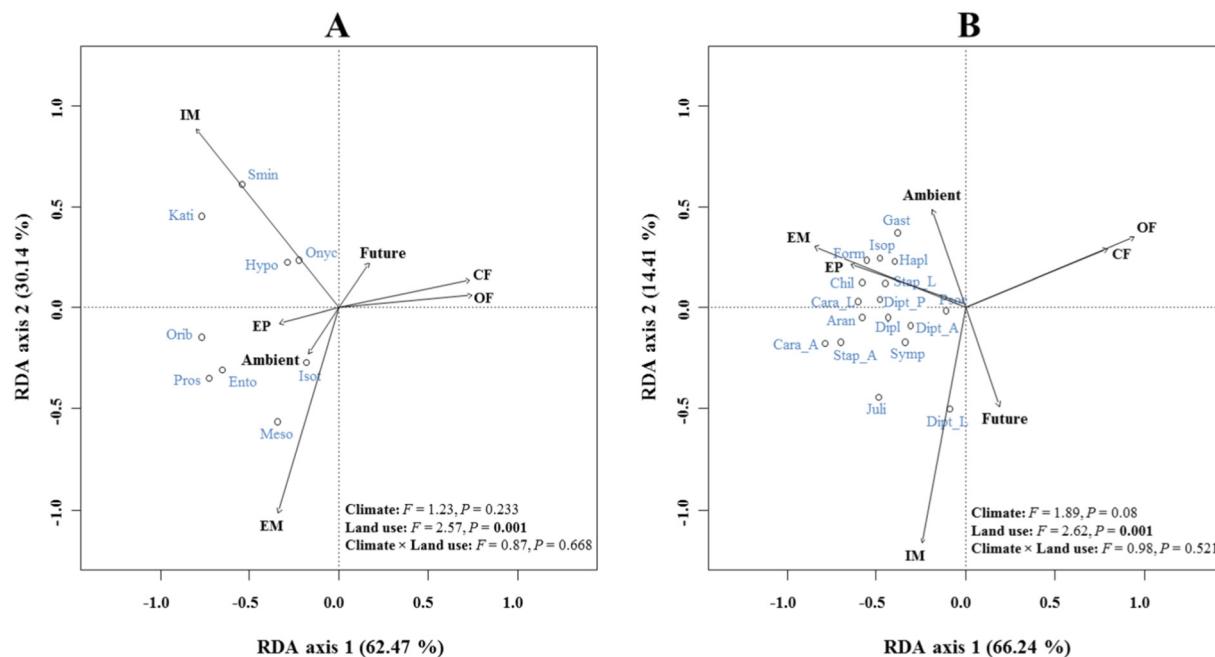


Fig. 4. A: Effects of climate and land use on community composition of mesofauna. B: Effects of climate and land use on community composition macrofauna. Notes: Results based on redundancy analyses (RDA), and arrows refer to two climate treatments (Ambient and Future), and five land-use regimes (for abbreviations see Fig. 1). Abbreviations for soil fauna groups (in alphabetical sequence): Aran: Araneae, Cara_A: Carabidae adult, Cara_L: Carabidae larvae, Chil: Chilopoda, Dipl: Diplura, Dipt_A: Diptera adult, Dipt_L: Diptera larvae, Dipt_P: Diptera pupae, Ento: Entomobryidae, Form: Formicidae, Gast: Gastropoda, Hapl: Haplotauxida, Hemi: Hemiptera, Hypo: Hypogastruridae, Isop: Isopoda, Isot: Isotomidae, Juli: Julida, Kati: Katiannidae, Meso: Mesostigmata, Onyc: Onychiuridae, Orib: Oribatida, Pros: Prostigmata, Psoc: Psocoptera, Smin: Sminthurididae, Stap_A: Staphylinidae adult, Stap_L: Staphylinidae larvae and Symp: Symphyla.

(Coleman et al., 2004), therefore, the absence of stronger effects of the precipitation changes on most of soil fauna groups in our experiment were surprising and in contrast to several other published studies (Blankinship et al., 2011; Kardol et al., 2011; Lindberg and Bengtsson, 2005). Eisenhauer et al. (2012) argued that in some cases fauna in the upper soil layers might have the capacity to adapt to drought events and may therefore be less vulnerable. Moreover, soil fauna may move to deeper soil layers during drought phases. Since we sampled soil fauna during the activity peaks in spring and autumn (which receive in contrast to the summer slightly more precipitation in the future climate treatment), we might have missed this specific effect of the stronger summer drought. Further, it might be speculated that one year of climate manipulation before the first sampling might be rather short to provoke changes in the abundance of soil fauna. However, generation times mainly range between a few days and a few months across the studied taxa (Table S9), which should allow several generations per year and therefore noticeable changes of population densities. Moreover, we could not find weaker climate effects on macrofauna with generally longer generation times. Nevertheless, it can be expected that the climate manipulation will cause accumulative changes in the biotic and abiotic environment with potentially stronger effects after several years.

In our experiment, the temperature increase in soil caused by roof closing during the night is about the same or may slightly exceed the increment of air temperatures near the soil surface. This somewhat surprising result can be explained by a reduced vegetation cover in this treatment as a consequence of the changed climate and thereby an increased exposure of the soil surface to direct insolation (Schädler et al., 2019). Night warming therefore increases soil temperature directly and indirectly via changes in the vegetation cover, which has to be considered as a realistic scenario rather than an artifact. This is also the case for other environmental variables which are directly or indirectly linked to the manipulated climate. For instance, we could demonstrate a longer frost-free period and an increase of growing degree days on plots with future climate due to the temperature manipulation

(Schädler et al., 2019), and both phenomena are important components of future climatic scenarios (Maracchi et al., 2005). In the case of relative air humidity, we found lower values on future climate plots even during the night, which is counterintuitive to the expected results of roof closing. Again, the realistic effect of a reduced vegetation cover is overriding the possible artifact of experimental manipulation in this case. Related to this, differences of effects of climate treatment between land-use regimes can also be assigned to mediating effects of the corresponding vegetation structure and cover. The proportion of bare soil as well as height and density of vegetation determine the level of temperature increase by night roofing in microhabitats in the vegetation and below the soil surface. This adds to the potentially interacting effects of climate and land use in real ecosystems. In sum, even a climatic condition with a rather small increase of the mean daily temperature has been shown to directly and indirectly affect soil fauna and also associated soil processes in this experiment (Yin et al., 2019). This should be kept in mind when critical thresholds of temperature increase and potential consequences are discussed (e.g., the “two degrees goal”, Rogelj et al., 2016).

4.2. Climate-independent land-use effects on soil fauna

The observed strong effects of land-use regimes on the soil fauna with lower abundance, lower number of taxa and changed composition in croplands compared to grasslands are in accordance with previous studies (Barrios et al., 2005; Foley et al., 2005; Muchane et al., 2012; Schmidt et al., 2015). Detrimental effects in croplands were shown to include clearing of native vegetation and the disturbance of the soil upper horizon, application of agrochemicals, mono-cropping, exposure to desiccation, limited access to food sources, and habitat modifications (Alvarez et al., 2001; Baker, 1998; Muchane et al., 2012). The responses of Collembolan families to land use differed in direction and magnitude. In line with a previous study (Cluzeau et al., 2012), the dominant family Isotomidae has been shown to be rather insensitive to land use, although significant land-use effects were found on total Collembola.

Our results suggest that land-use conversion from grasslands to croplands is an important driver of abundances of all orders of Acari, but not management intensity within the two land-use types. In part, these results are in line with those of Minor and Cianciolo (2007), who show that land-use types along an increasing intensity gradient negatively affected Oribatida but not Mesostigmata. Overall, we found Acari to be more sensitive to the changes of land use compared to Collembola. Accordingly, Acari are often regarded as good bioindicator for assessing the consequences of land-use change (Gulvik, 2007).

Further, most of the macrofaunal groups in this study (Coleoptera, Diplura, Isopoda and Formicidae) were more abundant in grasslands compared to croplands. Several previous studies showed that frequent disturbances due to intensive agricultural practices in croplands are detrimental to the macrofauna community in the soil, whilst the conditions in meadows and pastures can support high levels of diversity and abundance of these organisms (Barrios et al., 2005; Brévault et al., 2007; Muchane et al., 2012; Pauli et al., 2011; Tsiafouli et al., 2015). Furthermore, land-use effects on soil biota may also be mediated through indirect effects on microclimatic conditions. The soil water content showed no substantial differences between the land-use regimes in our study. However, the tendency of higher soil temperatures in the grasslands (Fig. S2) might positively affect soil fauna abundance. Microclimatic effects of land management can therefore be suggested to superimpose the effects of minor and moderate changes of ambient temperatures.

Most soil fauna groups showed strong variations between sampling dates which often interacted with land-use type. The mesofauna showed the highest abundances in spring 2016 and autumn 2016, mainly driven by Collembola. We can only speculate about the reasons for these variations, but they might be due to shifts in activity patterns in response to climatic differences. Macrofauna showed a distinct maximum at the last sampling date, which might be the result of the ongoing colonization of the former arable site.

The findings of De Vries et al. (2012) indicate that extensive land management buffers the effects of climate change on microbial soil food-webs. However, this could not be confirmed by our study on soil fauna, since no significant interaction effects between land-use regime and climate change were found on the abundance and community composition of soil fauna. Comparable studies are needed in the future to assess the generality of these findings.

5. Conclusions

Our study indicates that the effects of a predicted climate change scenario on soil fauna communities are minor, even though we found a negative overall effect on the abundances across all investigated taxa. Especially, abundances of few key taxa (e.g., Isotomidae and Chilopoda) decreased under the future climate scenario. Notably, these minor climate change effects were consistent across the five common land-use types in the region. Generally, meso- and macrofauna were more abundant in grasslands than in croplands. This might be caused by direct effects of management (e.g., disturbances, plant diversity), but also by indirect effects via a changed microclimate in soil. Within these land-use types, however, land-use intensity had minor effects. Taken together, these results suggest that land-use effects on soil fauna communities are equally strong under current and future climate conditions.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.apsoil.2019.03.026>.

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